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CABALLOID HORSES AND LATE MIDDLE PLEISTOCENE BIOSTRATIGRAPHY OF THE BRITISH ISLES

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Eline N. VAN ASPEREN

ABSTRACT

Over the last decades, researchers have become increasingly aware of the complexity of the Quaternary glacial - interglacial cycles. Correlation of continental sites with (sub)stages of the oxygen isotope record and with other sites has proven to be difficult. In order to be able to address questions that go beyond analysis of single sites it is necessary to have a rigid chronological framework.

For the British Isles, a biostratigraphic framework has been developed for the late Middle Pleistocene, incorporating geological, faunal and floral evidence. For the mammalian faunas, in particular, each interglacial stage was shown to have a characteristic fauna. The caballoid horse lineage undergoes a size reduction and morphological changes over its temporal range. These trends are well-documented for the Late Pleistocene. For the late Middle Pleistocene, the picture is less clear, in part because it has proven difficult to date sites from this period relative to each other. The robust and generally accepted biostratigraphic scheme for the British Isles provides an opportunity to address the evolution of the caballoid horses in the late Middle Pleistocene.

Keys-words: Equidae, biostratigraphy, late Middle Pleistocene, British Isles.

RÉSUMÉ

LES CHEVAUX CABALLINS ET LA BIOSTRATIGRAPHIE DU PLÉISTOCÈNE MOYEN RÉCENT DES ÎLES BRITANNIQUES

Ces dernières décennies, les chercheurs ont pris de plus en plus conscience de la complexité des cycles glaciaires et interglaciaires du Quaternaire. La corrélation des sites continentaux aux stades et sous-stades de la courbe isotopique de l'oxygène et à d'autres gisements s'est révélée être difficile. Afin de pouvoir aller au-delà de l'analyse ponctuelle de sites uniques, il est nécessaire d'avoir un cadre chronologique rigoureux.

Concernant les îles britanniques un cadre biostratigraphique a été développé pour le Pléistocène moyen récent, sur la base d'éléments relevant de la géologie, de la faune et de la flore. Pour les mammifères, en particulier, chaque interglaciaire est représenté par une faune caractéristique. La lignée des chevaux caballins voit sa taille se réduire et des changements morphologiques apparaître à travers le temps. Ces tendances sont bien documentées pour le Pléistocène récent. En revanche, pour le Pléistocène moyen récent, le schéma est moins précis, du fait de la datation relative difficile à appréhender entre les différents gisements. Le cadre biostratigraphique rigoureux et généralement bien accepté des îles britanniques fournit une opportunité pour mieux comprendre l'évolution des chevaux caballins lors du Pléistocène moyen récent.

Mots-clés : Equidés, biostratigraphie, Pléistocène moyen récent, îles britanniques.

1 - INTRODUCTION

The late Middle Pleistocene (≈ 400,000 - 125,000 years BP) in northwest-central Europe begins with the first major cooling of the Elsterian glaciation and ends at the beginning of the Eemian Interglacial (Turner, 1996; Gibbard & Van Kolfschoten, 2004). In the British Isles, the late Middle Pleistocene is defined as the period from the Anglian glaciation to the beginning of the Ipswichian Interglacial. Until recently, three glacials (the Anglian, Wolstonian and Devensian) and two interglacials (the Hoxnian and the Ipswichian) were recognised in the late Middle and Late Pleistocene of the British Isles, based mainly on the study of glacial sediments and pollen analysis (Mitchell *et al*., 1973). However, this forced mammal researchers to assume that the faunal assemblages dated to each of the warm stages were heterogeneous and that considerable changes have taken place both between and within the warm stages (Currant, 1989).

Over the last decades, increasing knowledge of the glacial-interglacial cycles as documented in the oxygen isotope record of foraminifera in deep-sea sediments (Emiliani, 1955; Shackleton & Opdyke, 1973) has led to the recognition that the climatic cycles of the late Middle Pleistocene were more complex than previously thought. Attempts to correlate the continental glacials and interglacials with marine oxygen isotope stages led to much research and discussion. Correlation of the Eemian and Ipswichian with oxygen isotope stage (OIS) 5e, based on direct correlation of oxygen isotope values of pollen-containing cores and absolute dating (e.g. Shackleton, 1969; Gascoyne *et al*., 1981; Turon, 1984; Sánchez Goñi *et al*., 2000), is generally accepted. Correlation of the conti-

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nental Saalian, Holsteinian and Elsterian with the oxygen isotope record, however, is still a matter of debate (for a recent overview of the debate see Geyh & Müller, 2005). However, the evidence seems to point to a correlation of the Holsteinian with the British Hoxnian. Because of the severity of the Anglian and the pronounced warm character of the Hoxnian, these periods are usually correlated with OIS 12 and OIS 11, respectively (Shackleton, 1987; various authors in Bowen, 1999; Gibbard *et al*., 2004). This implies the presence of two previously unrecognised temperate periods, OIS 9 and OIS 7, between the Holsteinian / Hoxnian and the Eemian / Ipswichian.

In the British Isles, evidence for these additional temperate periods has come from terrace stratigraphy, mammalian faunas and amino acid stratigraphy (Bridgland, 1994; Schreve, 1997; Penkman, 2005). Because of the contested nature of the correlation of the Holsteinian with OIS 11 and the apparent lack of sites dating from OIS 9 and OIS 7, correlation of sites from the European mainland with the deep-sea oxygen isotope record remains problematic. The chronostratigraphy of the late Middle Pleistocene of the British Isles, on the other hand, is robust and generally accepted. Study of the British faunas can thus provide a template for the study of faunas from the European mainland.

2 - BIOSTRATIGRAPHY OF THE BRITISH ISLES

The Anglian glaciation caused the diversion of the River Thames from a more northerly course into its present valley (Bridgland, 1994). This diversion was followed by incision due to progressive uplift, leading to the development of a terrace staircase (Maddy & Bridgland, 2000). In the Lower Thames valley, four terraces have been recognised above the current floodplain, with temperate deposits occurring in each of the four terraces (Bridgland, 1994, see fig. 1). These interglacial deposits are considered equivalent to OIS 11, 9, 7 and 5e, respectively. Based on an analysis of the mammal faunas from the Lower Thames terraces, Schreve (1997) formulated a biozonation for the British late Middle Pleistocene. Each interglacial is characterised by a distinct fauna, but due to the severity of the climate during a large part of the glacial stages, the glacial faunas are poorly known. Similar results have been obtained for the terrace sequences and corresponding faunas of other British rivers (Schreve, 1997; Bridgland & Schreve, 2001). Recent developments in amino acid geochronology have led to corroboration of the biostratigraphic scheme (Penkman, 2005).

Due to their geographical location, the British Isles underwent drastic fluctuations in climatic conditions during the glacial-interglacial cycles of the late Middle Pleistocene. In addition, short periods of insularity are postulated for at least some of the interglacial periods concerned. From evidence of raised beaches, estuarine influences in the rivers and molluscan and vertebrate faunas it seems likely that a southern connection between the North Sea and the Atlantic Ocean existed during the warmest parts of OIS 5e and OIS 7, and probably OIS 9 (Keen, 1995; Sutcliffe, 1995; White & Schreve, 2000). Temperate and cold-adapted species migrated in and out of the British Isles throughout the late Middle Pleistocene, limited in their movement and isolated from conspecifics on the European mainland by periods of insularity. In some periods, a reduced diversity and specific adaptive responses differentiate the British faunas from those of mainland Europe (Schreve & Bridgland, 2002). The potential for observable differences between the faunas of the various interglacial stages is therefore high.

The influence that strong environmental fluctuations and periods of insularity exerted on the composition and adaptations of the mammal fauna limits the application of the faunal data to the British Isles. However, the good

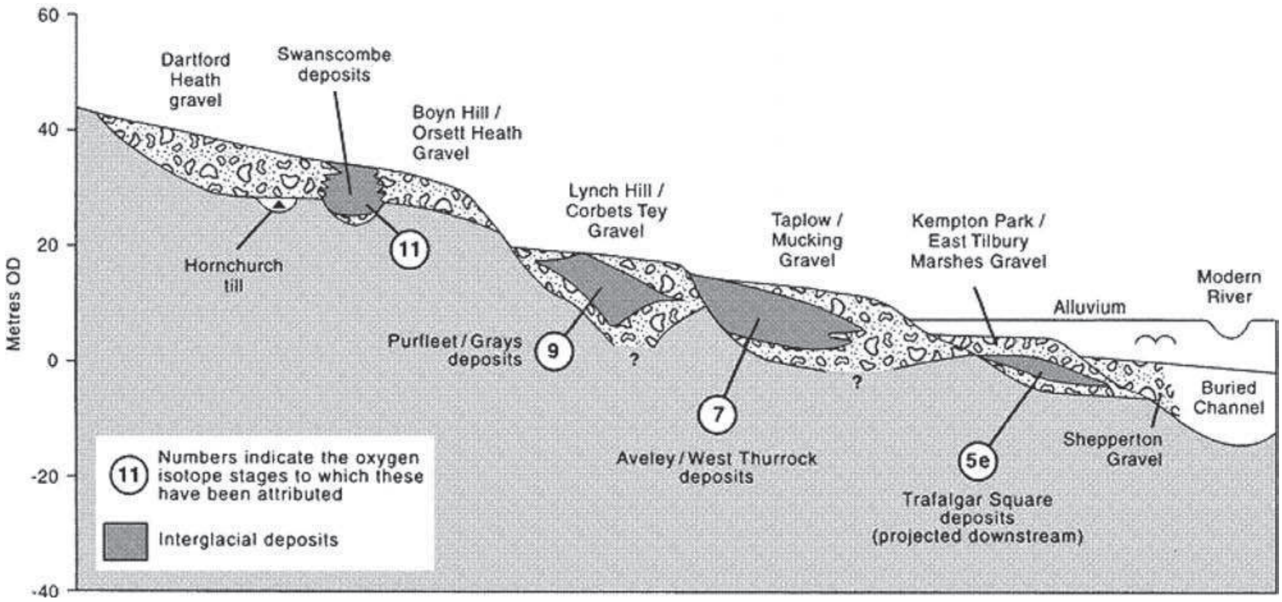

Fig. 1: Idealised transverse section through the Lower Thames terrace sequence, showing the stratigraphical position of interbedded interglacial sediments, with their proposed correlations with the oxygen isotope record. Modified from Bridgland, 1994.
Fig. 1 : Section transverse idéalisée de la Tamise, montrant la position stratigraphique des sédiments interglaciaires associés et la corrélation proposée avec les données obtenues à partir de la courbe isotopique de l'oxygène. Modifiée d'après Bridgland, 1994.

chronostratigraphic control, paired with ample environmental information, can be utilised to assess the way in which various species adapted to changing environments through time. This knowledge can then be used to analyse the adaptations of the same species on the European mainland, and can aid in the development of a biostratigraphic framework for other parts of Europe.

3 - MIDDLE PLEISTOCENE CABALLOID HORSES

The caballoid horse lineage is one of the few large mammal lineages that show a clear evolutionary trend during the Pleistocene. Remains of horses occur in abundance on many important late Middle Pleistocene archaeological and palaeontological sites. Horses are wide- ranging geographically, have a high dispersal potential and occurred both in warm and in cold periods. These characteristics greatly enhance their usefulness for biostratigraphic purposes (Savage, 1977; Lister, 1992). Caballoid or true horses are thought to have evolved from the more primitive stenonid horses during the Early Pleistocene (Forstén, 1988). During the early Middle Pleistocene, caballoid horses became more numerous and gradually replaced the various stenonid species in Europe.

The evolution of the caballoid horse lineage during the Late Pleistocene in Europe has been the subject of much research, with some research extending into the Middle Pleistocene (e.g. Nobis, 1971; Eisenmann, 1991a, b; Forstén, 1993). The Late Pleistocene horses are characterised by a decrease in size, with a reduction in size in the limb bones becoming apparent from 100,000 years ago, and a possible decrease in size of the dental elements from 200,000 years ago (Eisenmann, 1991b). In addition to changes in size, changes in shape took place, especially morphological changes in the metapodials and phalanges as a result of the increasing adaptation of the equids to a cursorial way of life, which led to monodactyly through the reduction of the lateral toes, a loss of flexibility in the foot and the development of the automatic spring mechanism (Sondaar, 1968; MacFadden, 1992).

During the Middle Pleistocene, horse size fluctuated around a mean with no net trend, implying evolutionary stasis (Forstén, 1993). Fluctuations in size and shape are expected as ecophenotypic responses to the rapidly changing environments of the Pleistocene. Studies of later horse populations have shown that, although the caballoid horses are relatively homogeneous in their morphology, there is variation between local populations which might be related to adaptations to local conditions (Forstén, 1993; Bignon, 2003, 2008). The size fluctuations and the morphological adaptations of the caballoid horses can therefore be of use for the biostratigraphy of the late Middle Pleistocene of the British Isles. A complicating feature of horse size and shape is that, although the minimum and maximum size to which an individual can grow is under genetic control, many factors can influence the size and shape of the bones. These factors include age, sex, genotype, genetic exchange, migration, physical condition, habitat quality, temperature, humidity, population size, inter- and intra-specific competition and predation. It should be kept in mind that animals generally experience a variety of selection pressures at the same time, and different selection pressures can select for similar characteristics or adaptations.

An analysis of the differences and similarities between horse remains from different oxygen isotope stages might shed light on the influence of the factors listed above on the size and shape of the bones. Research on the British horse material can also aid in assessing the potential of horse material for answering biostratigraphical questions, and indicate whether horse material could be of use in distinguishing between sites of different oxygen isotope stages in continental Europe.

4 - MATERIAL AND MEASUREMENTS

From each interglacial and from two glacial stages of the British late Middle Pleistocene, faunal assemblages are now known, and each stage yielded sites with horse remains. Some of the remains come from old collections of amateur palaeontologists, other remains were recovered in controlled excavations (see tab. 1 for a list of sites with numbers of analysed remains and fig. 2 for the

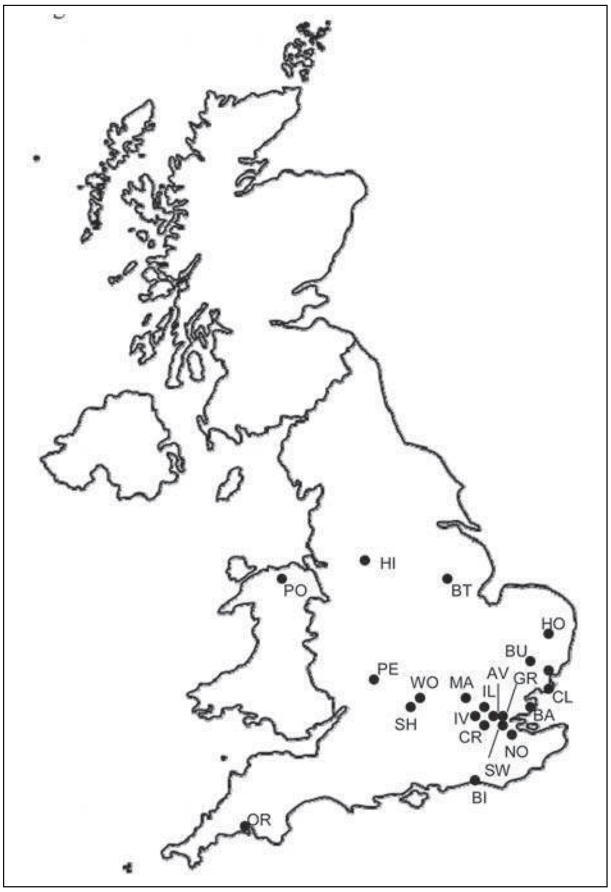

Fig. 2: Location of sites studied. AV = Aveley, BA = Barling, BI = Brighton, BT = Balderton, BU = Brundon, CL = Clacton, CR = Crayford, GR = Grays Thurrock, HI = Hindlow, HO = Hoxne, IL = Ilford, IV = Ingress Vale, MA = Marsworth, NO = Northfleet, OR = Oreston, PE = Pershore, PO = Pontnewydd, SH = Stanton Harcourt, ST = Stoke Tunnel, SW = Swanscombe, WO = Wolvercote
Fig. 2 : Localisation des sites étudiés.

OIS	Site	p2	p3/4	m1/2	m3	P2	P3/4	M1/2	M3	mc	mt	ph1ant	ph1post
11	Swanscombe		5	9	4		8	7	1	2			
	Ingress Vale						1	1	1				
	Clacton		1	1	1	1	1	4	1	1	2	2	
	Hoxne	2	10	11	10	6	10	10	3	2		1	
9	Grays Thurrock	1	4	10	6	4	8	11	3	1			3
	Pershore	1	3	8	2			4	1	5	4	3	3
	Wolvercote	3	6	7	4	2	1	2			4	3	
8	Barling						1			5	12	1	
7	Aveley	2	4	4	1	2	4	8	3		1	1	
	Northfleet		1	1	2			3				1	
	Stanton Harcourt										1	1	
	Ilford	2	5	4	2	1	5	7		5	6	2	4
	Crayford	3	15	10	7	2	13	14	3	9	15	8	8
	Brundon	2	8	10	4	3	4	8	4	9	22	2	3
	Stoke Tunnel			2			6	6	3	3	1	4	1
	Marsworth OIS 7	6	11	11	12	8	14	20	2	9	6	6	6
	Pontnewydd		6	2		1	2	1	3		3	5	
	Oreston	5	9	14	5	3	9	12	2	1		4	1
	Hindlow	2	2	1	1	2	2	2	1	4	1	2	1
6	Marsworth OIS 6	2	2	1	1	3	6	11	1	3	3	2	7
	Balderton			1			1	3	1	5	14	4	5
	Brighton	1	8	11	5	3	9	15	3	3	8	1	3

Tab. 1: Sites and numbers of analysed remains. mc = metacarpals, mt = metatarsals, ph1ant = anterior first phalanges, ph1post = posterior first phalanges.
Tab. 1 : Sites et nombre des spécimens analysés. mc = métacarpiens, mt = métatarsiens, ph1ant = premières phalanges antérieures, ph1post = premières phalanges postérieures.

location of the sites). The provenance of some of the material from these sites is unclear, and only material that could with certainty be attributed to the interglacial or glacial concerned was included in this research. The interglacial material is correlated with OIS 11 (Hoxnian), OIS 9 (Purfleet interglacial) and OIS 7 (Aveley interglacial). Horses are noticeably absent from OIS 5e (Ipswichian) faunas in the British Isles. Two glacial periods, OIS 8 and OIS 6, also produced sites with horse remains. Horse remains from the British Isles dating from this time period are commonly referred to *Equus* sp. or *Equus ferus*.

Dental elements, metapodials and first phalanges were analysed for size and shape differences. These elements are relatively numerous in fossil assemblages, and exhibit specific adaptations to diet and locomotion. In addition, they underwent long-term evolutionary developments. Dental elements are expected to be less variable than limb bones, as the former are under genetic control, whereas the latter are more environmentally plastic (Hillson, 2005). Horses display very little sexual dimorphism or adult age variation (MacFadden, 1992), and only the permanent dentition and leg bones with fully fused epiphyses were used in this study.

Measurements on the metapodials were taken according to Eisenmann (1979) and measurements on the first phalanges follow Dive & Eisenmann (1991). For the dental material, length, width and height, and in the upper third and fourth premolars and upper first and second molars the length of the protocone, were measured according to Musil (1969). Furthermore, the ratio of protoconal length to total length was calculated for upper premolars and molars (protoconal index or IP, Lprot / L x 100%). Since it is very difficult to distinguish between the third and fourth premolar and between the first and second molar, especially in isolated specimens, these are analysed together, as third / fourth premolar and first / second molar respectively. All measurements were taken with vernier callipers and recorded to the tenth of a millimetre. In the following sections, the maxillary dentition will be indicated as P2-4 and M1-3 and the mandibular dentition will be indicated as p2-4 and m1-3. Measurements on the metapodials and the first phalanges will be abbreviated with "V", e.g. V1 = variable 1.

5 - STATISTICAL METHODS

Since a fundamental aim of this study is to investigate whether assemblages of horse remains from different oxygen isotope stages can be distinguished from each other based on their size and shape, the data were divided into groups based on the attribution of the remains to specific oxygen isotope stages. Statistical analyses were performed with the Statistical Package for the Social Sciences (SPSS) version 15.0. The sample of each oxygen isotope stage was tested for normality with the Shapiro-Wilk test when $n \leq 50$ and the Kolmogorov-Smirnov test when $n > 50$. Hereinafter, it can be assumed that all data are normally distributed unless specified otherwise. When appropriate, non-parametric tests were used. Differences between the

OIS	L P2	W P2	n (max)	L P3/4	W P3/4	Lprot P3/4	n (max)	L M1/2	W M1/2	Lprot M1/2	n (max)	L M3	W M3	n (max)
11	40.6	28.4	7	31.7	30.2	14.2	20	30.4	28.6	13.8	23	30.9	25.0	6
9	39.0	29.4	6	31.8	30.8	14.4	9	30.4	27.5	14.8	17	35.6	26.7	4
7	39.7	27.2	21	31.2	29.3	14.0	58	29.6	28.7	14.9	80	32.0	25.2	21
6	38.8	24.9	6	28.2	26.6	14.0	16	27.6	25.8	13.6	29	28.1	21.2	5

Tab. 2: Mean values of measurements on the maxillary dentition of Middle Pleistocene horses from the British Isles.
Measurements according to Musil (1969); L = length, W = width, Lprot = length of the protocone.
Tab. 2 : Valeurs moyennes des dimensions des dents jugales supérieures des chevaux du Pléistocène moyen des îles britanniques. Mesures d'après Musil (1969) ; L = longueur, W = largeur, Lprot = longueur du protocone.

morphology of horses of the different oxygen isotope stages were tested using one-way analysis of variance (one-way ANOVA) for data that were normally distributed, and the Kruskal-Wallis test for non-normally distributed data. This was repeated for each element (maxillary dentition, mandibular dentition, metacarpals, metatarsals, anterior and posterior phalanges). Where a posteriori tests were appropriate (i.e. for those analyses in which the ANOVA showed a significant difference), Tukey's HSD test was used for data in which variances were homogeneous, and Tamhane's T2 multiple comparison test was used for samples with unequal variances. Results for all the tests were considered to be significant if $p \leq 0.05$.

The data on the leg bones were analysed using log ratio diagrams. The log ratio technique was introduced for palaeontological material by Simpson (1941). Log ratio diagrams represent various measurements on the same anatomical element in such a way that the vertical distances between the different measurements express their relative sizes (the ratios of their dimensions). Another result of converting absolute measurements to logarithms is an exaggeration of small values and a minimisation of large values, making it easier to compare the ratios of different specimens (Simpson *et al.*, 1960). In order to create a log ratio diagram, all measurements are converted to their logarithms. One specimen or group of specimens is taken as the standard of comparison, representing the base line or reference line of the diagram. In this study, the standard chosen is a sample of *Equus hemionus*, as this is the species most commonly used as a standard for log ratio diagrams of Pleistocene horse remains (e.g. Eisenmann, 1979; Dive & Eisenmann, 1991). For the other specimens or groups of specimens, the difference between their logarithmic values and the logarithmic values of the standard is calculated and plotted on a graph. A line is drawn to connect the values of the different measurements for each specimen or group of specimens, and the closer the lines are in a vertical aspect, the more similar the size of the specimens. Similarity in the profile of the lines reflects similarity in the proportions of the specimens. The order in which the measurements appear in the diagrams is chosen according to their usefulness in comparing different samples and the differential survival of different parts of the bone, such that measurements that often cannot be taken on incomplete specimens are at both ends of the axis (Eisenmann 1979).

6 - RESULTS

6.1 - MAXILLARY DENTITION (TAB. 2 & 3)

There is no material from OIS 8. The lengths of the M1/2 of OIS 7 and the protoconal lengths of the M1/2 of OIS 6 are not normally distributed (OIS 7 LM1/2: n = 77, Kolmogorov-Smirnov test statistic = 0.122, df = 77, p = 0.006; OIS 6 LprotM1/2: n = 28, Shapiro-Wilk test statistic = 0.925, df = 28, p = 0.047). The Kruskal-Wallis test is significant for both measurements (LM1/2: n = 139, chi-square = 20.542, df = 3, p = 0.000; Lprot M1/2: n = 138, chi-square = 11.595, df = 3, p = 0.009). The ANOVA indicates that there is a significant difference between the samples of the different oxygen isotope stages for all elements except the lengths of the P2 and the protoconal lengths of the P3/4 (tab. 4). The post-hoc tests indicate significant differences in all measurements between the material of OIS 6 and the

OIS	IP P3/4	IP M1/2	Type
11	44.8	45.4	III
9	45.3	48.7	I
7	44.9	50.3	I
6	49.6	49.3	II

Tab. 3: Protoconal indices (IP) of the maxillary dentition.
Tab. 3 : Indices protoconiques des dents jugales supérieures.

	Measurement	n	F	p
Maxillary dentition	LP2	38	0.585	0.629
	WP2	40	7.029	0.001
	LP3/4	98	9.915	0.000
	WP3/4	93	8.771	0.000
	LprotP3/4	94	0.140	0.936
	WM1/2	137	14.645	0.000
	LM3	35	4.965	0.006
	WM3	32	4.761	0.008
Mandibular dentition	Lp2	30	1.402	0.265
	Wp2	31	1.277	0.302
	Lp3/4	88	6.668	0.000
	Wp3/4	100	2.685	0.051
	Lm1/2	111	3.682	0.014
	Lm3	63	3.792	0.015
	Wm3	65	1.413	0.248

Tab. 4: Results of ANOVA of measurements on the dentition (data from tables 2 & 5).
Tab. 4 : Résultats de l'ANOVA à partir des dents jugales (données des tableaux 2 & 5).

material of all other oxygen isotope stages, except for the widths of the M1/2 and both the lengths and widths of the M3, for which there is no significant difference between the material of OIS 11 and OIS 6.

Differences in the protoconal indices (IP) of the upper premolars and molars have been correlated with specific climatic trends (Eisenmann, 1991b). Relatively short protocones result in a low IP, whereas relatively long protocones result in a high IP. Eisenmann (1991b) characterised three types of caballoid horses based on their protoconal indices. Type I horses have shorter protocones on the P3/4 than on the M1/2, and are generally found in temperate climates. Horses of Type II have relatively long protocones on the P3/4 and relatively short protocones on the M1/2, and are often correlated with cold climatic conditions. Type III horses are characterised by short protocones on the P3/4 and especially on the M1/2. These horses occur in cold to cool environments. However, these environmental correlations cannot be regarded uncritically, as there is currently no functional model to correlate the relative length of the protocone to environmental adaptations.

The protoconal indices (IP) of the British late Middle Pleistocene horse P3/4 and M1/2 are varied (tab. 3). The indices of the OIS 11 dental elements are typical of Type III, whilst those of the OIS 9 and OIS 7 material are indicative of Type I. The indices of the OIS 6 horses are ambiguous, but since only horses of Type II have long protocones on the P3/4, the OIS 6 material is attributed to this type.

For all elements, the material from OIS 6 is smaller in size than that of the other three oxygen isotope stages. In the data for the P3/4 and the M1/2, the material of OIS 11, 9 and 7 clusters together. The P2 data show a decrease in size from OIS 11 to OIS 7, but the P2 of OIS 9 is relatively wide. In the data for the M3, the material of OIS 11 and 7 forms a cluster, with the OIS 9 material being clearly broader.

6.2 - MANDIBULAR DENTITION (TAB. 5)

There is no material from OIS 8. The widths of the m1/2 of OIS 6 are not normally distributed (n = 13, Shapiro-Wilk test statistic = 0.849, df = 13, p = 0.028). The Kruskal-Wallis test produces a significant result for this measurement (n = 116, chi-quare = 18.668, df = 3, p = 0.000). The ANOVA produces a significant result for the lengths of the p3/4, the m1/2 and the m3 (table 4). The results of the post-hoc tests show that the differences concentrate on the material of OIS 6, although the lengths of the m1/2 are significantly different between the OIS 11 and the OIS 9, 7 and 6 material.

Again it can be observed in all elements that the material from OIS 6 is smaller in size than that of the other three oxygen isotope stages. In the data for the p3/4 and the m3, the data for OIS 11, 9 and 7 cluster together. The data for the p2 of OIS 9 and 7 are clustered and are characterised by relatively narrow widths. The data for the m1/2 also shows a clustering of the OIS 9 and 7 material, with the OIS 11 material being larger.

6.3 - METACARPALS (TAB. 6)

The data for V3 on the OIS 6 material are not normally distributed (n = 10, Shapiro-Wilk test statistic = 0.819, df = 10, p = 0.025). The Kruskal-Wallis test is significant for this measurement (n = 63, chi-square = 15.815, df = 4, p = 0.003). The ANOVA indicates that there is a significant difference in all measurements between metacarpals from different oxygen isotope stages (tab. 7). Two clusters of data emerge from the post hoc tests: there are no significant differences between OIS 11, 8 and 7 on

OIS	Lp2	Wp2	n (max)	Lp3/4	Wp3/4	n (max)	Lm1/2	Wm1/2	n (max)	Lm3	Wm3	n (max)
11	35.1	19.0	2	32.1	19.2	16	31.4	18.3	21	36.0	15.4	15
9	34.1	16.6	5	30.5	20.0	13	29.1	17.6	25	35.0	15.6	12
7	34.4	16.9	22	31.0	19.4	61	29.6	17.5	59	35.0	15.0	34
6	31.6	17.2	3	29.2	17.9	10	28.8	15.6	13	31.5	14.3	6

Tab. 5: Mean values of measurements on the mandibular dentition of Middle Pleistocene horses from the British Isles.
Measurements according to Musil (1969); L = length, W = width.
Tab. 5 : Valeurs moyennes des dimensions des dents jugales inférieures des chevaux du Pléistocène moyen des îles britanniques. Mesures d'après Musil (1969) ; L = longueur, W = largeur.

	n (max)	V1	V3	V4	V5	V6	V10	V11	V12	V13	V14	V7	V8
E. hemionus	22	214.1	25.7	21.1	43.2	27.0	38.9	38.7	29.3	24.3	26.1	34.0	12.8
OIS 11	5	241.8	39.6	29.3	55.4	37.6	53.1	54.2	40.6	32.4	34.0	46.4	16.5
OIS 9	6	221.9	36.6	27.1	48.7	32.1	47.8	46.8	36.7	28.7	30.9	39.5	14.7
OIS 8	5	246.3	39.9	30.2	56.2	37.4	51.9	51.5	38.0	31.8	34.2	45.6	18.0
OIS 7	40	237.4	40.1	29.8	56.7	37.9	53.8	55.0	41.0	32.3	34.0	46.5	17.9
OIS 6	6	219.8	36.3	27.0	53.0	35.9	47.7	49.1	34.7	28.8	29.3	44.9	16.0

Tab. 6: Mean values of measurements on the metacarpals of *Equus hemionus* (Eisenmann, 1979: 881) and Middle Pleistocene horses from the British Isles.
Measurements according to Eisenmann (1979).
*Tab. 6 : Valeurs moyennes des dimensions des métacarpiens d'*Equus hemionus *(Eisenmann, 1979 : 881) et des chevaux du Pléistocène moyen des îles britanniques. Mesures d'après Eisenmann (1979).*

Measurement	n	F	p
V1	48	6.210	0.000
V4	63	7.094	0.000
V5	48	4.564	0.004
V6	49	9.218	0.000
V10	53	12.747	0.000
V11	49	19.014	0.000
V12	39	9.123	0.000
V13	50	8.253	0.000
V14	42	10.188	0.000
V7	49	7.772	0.000
V8	43	3.201	0.023

Tab. 7: Results of ANOVA of measurements on the metacarpals (data from table 6).
Tab. 7 : Résultats de l'ANOVA à partir des métacarpiens (données du tableau 6).

the one hand and few between OIS 9 and 6 on the other hand. The differences of OIS 11 and 7 with OIS 9 concern length and both the proximal and distal epiphyses. The differences of OIS 11 and 7 with OIS 6 concentrate on the distal epiphysis. The differences of OIS 8 with OIS 9 and 6 are relatively small and can be found in the proximal epiphysis.

The results of the statistical analysis are reflected in the log ratio diagram (fig. 3). The first aspect to note is that the two clusters of data that stand out in the statistical analysis also stand out in the diagram: the material of OIS 11, 8 and 7 is larger than that of OIS 9 or 6 on an absolute scale for all measurements. The material of OIS 11, 8 and 7 is similar in shape. The distal keel is relatively more developed in the OIS 11 and 7 material (V12, 13 and 14), and much less so in the OIS 8 material.

The metacarpals of OIS 9 are relatively narrow proximally (V5, 7). The sagittal keel of the distal epiphysis is relatively well-developed (V12, 13 and 14). The material has some primitive evolutionary features, with a large breadth over the supra-articular tuberosities relative to the breadth of the distal epiphysis (V10 and 11). This seems to be a reversal of the long-term evolutionary trend of reduction in breadth over the supra-articular tuberosities (Eisenmann, 1979). In the OIS 11 material, the breadth of the epiphysis is relatively large, and in the OIS 8 material, this breadth is increasing again, in OIS 7 leading to horses with a distal epiphysis of similar shape to those of OIS 11. The relatively narrow articular surface for the magnum (V7) is another primitive feature found in the OIS 9 material.

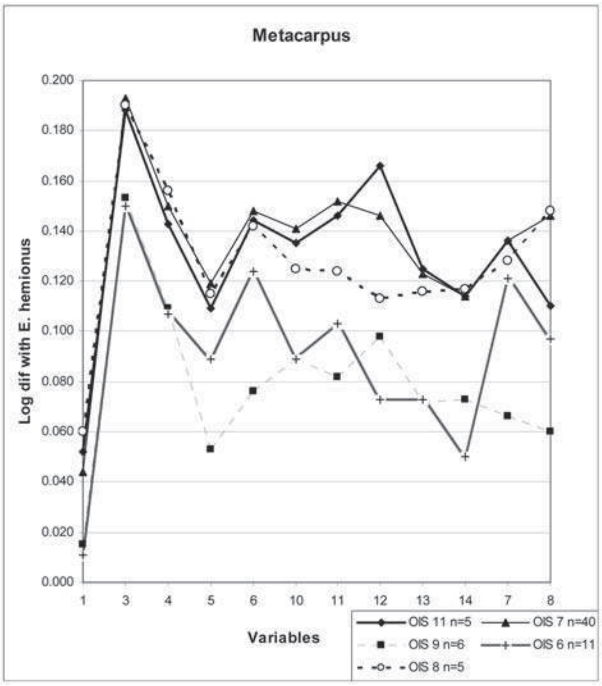

Fig. 3: Log ratio diagram of metacarpals from the British Isles.
Reference line: *Equus hemionus* (data from table 6).
Fig. 3 : Diagramme des rapports des métacarpiens des îles britanniques. Ligne de référence : Equus hemionus *(données du tableau 6).*

The material of OIS 6 is small in size and relatively robust, characterised by large breadths (V5, 7 and 11) relative to length (V1), and a strongly developed proximal epiphysis (V5, 6 and 7). However, the breadth over the supra-articular tuberosities (V10) is relatively small as a result of the long-term evolutionary trend of reduction in breadth over the supra-articular tuberosities. In the same context, the large size of the articular surface for the magnum (V7) should be noted.

6.4 - METATARSALS (TAB. 8)

There is insufficient material available for OIS 11 to merit a statistical analysis, therefore the OIS 11 sample is not included in the statistical analysis. The data for V3 on the OIS 7 material are not normally distributed (n = 46, Shapiro-Wilk test statistic = 0.895, df = 46, p = 0.001). The data for V3 are compared using the Kruskal-Wallis test, which yields a significant result (n = 87, chi-square = 26.541, df = 3, p = 0.000). The ANOVA indicates significant differences between the samples of the

	n (max)	V1	V3	V4	V5	V6	V10	V11	V12	V13	V14	V7	V8
E. hemionus	22	250.6	25.2	25.3	40.5	35.1	38.0	37.5	30.0	23.9	26.5	35.9	9.0
OIS 11	2	289.3	35.4	34.8	60.1	48.8	59.4	57.8	45.1	34.8	38.4	53.8	15.4
OIS 9	8	274.0	34.5	32.1	54.0	43.7	49.0	49.0	34.7	26.6	29.9	48.4	13.0
OIS 8	12	287.6	38.4	36.6	56.0	48.0	55.3	55.3	41.5	31.8	34.1	51.8	12.4
OIS 7	56	281.0	38.8	36.0	58.0	48.1	57.0	55.7	42.5	32.3	35.3	51.3	13.0
OIS 6	25	258.9	34.7	31.9	53.2	42.9	50.0	49.0	38.4	30.4	32.0	47.7	13.1

Tab. 8: Mean values of measurements on the metatarsals of *Equus hemionus* (Eisenmann, 1979: 881) and Middle Pleistocene horses from the British Isles.
Measurements according to Eisenmann (1979).
*Tab. 8 : Valeurs moyennes des dimensions des métatarsiens d'*Equus hemionus *(Eisenmann 1979: 881) et des chevaux du Pléistocène moyen des îles britanniques. Mesures d'après Eisenmann (1979).*

different oxygen isotope stages for all analysed measurements, except for V8 (tab. 9). The post-hoc tests again indicate that the data for OIS 8 and OIS 7 cluster, with a second cluster being formed by the data for OIS 9 and OIS 6. There are relatively few differences between OIS 9 and OIS 8. The differences between OIS 9 and OIS 7 can be found in both epiphyses, whereas OIS 8 and 7 differ from OIS 6 both in the epiphyses and in length.

In the log ratio diagram (fig. 4), it is apparent that the horse metatarsals of OIS 6 are again of small size. The length of the OIS 9 material is closer to those of the other oxygen isotope stages, but most other dimensions are clearly smaller. There are more differences in shape than in the metacarpals, with the material of OIS 8 and OIS 7 being the most similar in shape.

Since the graph of OIS 11 is based on only two specimens, one of which is incomplete, conclusions based on this material should be regarded as preliminary. The

Measurement	n	F	p
V1	59	10.170	0.000
V4	85	11.092	0.000
V5	67	8.234	0.000
V6	73	12.443	0.000
V10	64	19.583	0.000
V11	61	14.599	0.000
V12	59	7.444	0.000
V13	67	12.425	0.000
V14	62	8.401	0.000
V7	67	6.467	0.001
V8	61	.0210	0.889

Tab. 9: Results of ANOVA of measurements on the metatarsals (data from table 8).
Tab. 9 : Résultats de l'ANOVA à partir des métatarsiens (données du tableau 8).

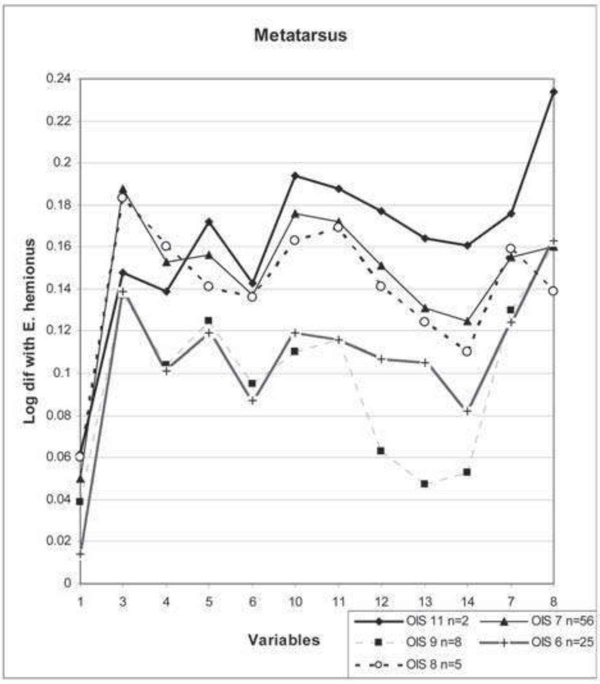

Fig. 4: Log ratio diagram of metatarsals from the British Isles.
Reference line: *Equus hemionus* (data from table 8).
Fig. 4 : Diagramme des rapports des métatarsiens des îles britanniques. Ligne de reference : Equus hemionus *(données du tableau 8).*

available material has a relatively slender diaphysis (V3 and 4), a broad proximal epiphysis (V5) and a well-developed distal epiphysis (V10, 11, 12, 13 and 14). As a primitive evolutionary feature, the facet that articulates with the ectocuneiform (V7) is relatively weakly developed on the single metatarsal on which this measurement could be taken.

The metatarsals of OIS 9 have relatively small depths (V4 and 6). The distal keel is not well-developed (V12, 13 and 14), but the breadth over the supra-articular tuberosities is small relative to the breadth of the distal epiphysis (V10 and 11). Another evolutionarily advanced feature is the large facet for the ectocuneiform (V7).

The diaphysis of the material of OIS 8 and 7 is relatively broad (V3), but both the proximal epiphysis and the distal sagittal keel are weakly developed (V5, 6, 12, 13 and 14). The facet that articulates with the ectocuneiform (V7) is fairly large. In the OIS 6 material, breadths are relatively large (V3 and 5) whereas depths are relatively small (V4 and 6). The articular facet for the ectocuneiform is fairly large (V7). The distal epiphysis is relatively strongly developed (V11, 12, 13 and 14).

6.5 - ANTERIOR FIRST PHALANGES (TAB. 10)

There is no material from OIS 8. For most measurements on the OIS 11 material, there are insufficient data to test for normality. The data for V6 on the OIS 9 material are not normally distributed (n = 4, Shapiro-Wilk test statistic = 0.759, df = 4, p = 0.047), and these data are therefore compared using the Kruskal-Wallis test, which produces a non-significant result. The ANOVA indicates significant differences in the data for V1, 4, 5 and 12 (tab. 11). The post-hoc test for these data shows significant differences between OIS 7 and OIS 6 and between OIS 11 and OIS 7 and 6 in the length measurements.

From the log ratio diagram (fig. 5), it is obvious that the phalanges of the different periods are similar both in

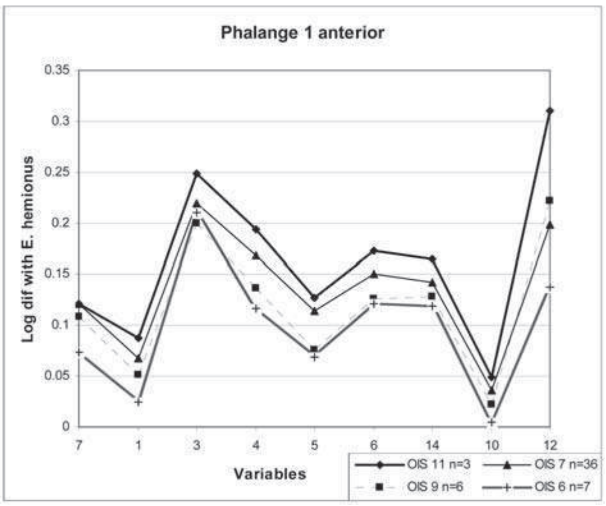

Fig. 5: Log ratio diagram of anterior first phalanges from the British Isles.
Reference line: *Equus hemionus* (data from table 10).
Fig. 5 : Diagramme des rapports des premières phalanges antérieures des îles britanniques. Ligne de reference : Equus hemionus *(données du tableau 10).*

		n (max)	V7	V1	V3	V4	V5	V6	V14	V10	V12
Anterior phalanges	*E. hemionus*	15	48.1	76.5	24.6	41.1	30.8	36.7	35.6	58.5	10.3
	OIS 11	3	63.5	93.5	43.5	64.3	41.3	54.6	52.0	65.4	21.1
	OIS 9	6	61.7	86.1	38.8	56.3	36.7	49.0	47.8	61.5	17.2
	OIS 7	36	63.5	89.6	40.6	60.6	40.1	51.8	49.3	63.6	16.3
	OIS 6	7	57.0	80.9	39.8	53.8	36.1	48.4	46.8	59.1	14.2
Posterior phalanges	*E. hemionus*	15	41.8	71.2	24.3	42.4	30.9	35.0	33.3	52.2	12.0
	OIS 9	6	59.0	86.7	39.5	60.4	40.5	49.9	47.7	60.9	17.9
	OIS 7	24	59.5	88.8	41.6	63.8	43.3	53.8	50.5	60.7	18.5
	OIS 6	15	51.7	76.9	37.3	56.2	38.7	46.8	44.7	52.4	15.6

Tab. 10: Mean values of measurements on the anterior and posterior first phalanges of *Equus hemionus* (Dive & Eisenmann, 1991: 292) and Middle Pleistocene horses from the British Isles.
Measurements according to Dive & Eisenmann (1991).
*Tab. 10. Valeurs moyennes des dimensions des premières phalanges antérieures et postérieures d'*Equus hemionus *(Dive & Eisenmann, 1991 : 292) et des chevaux du Pléistocène moyen des îles britanniques. Mesures d'après Dive & Eisenmann (1991).*

size and in shape, although the relative sizes follow a similar pattern as in the metapodials. The OIS 6 horses have a relatively deep proximal epiphysis (V5). The OIS 11 and 9 material has relatively long infra-tuberosital segments (V12), which is a primitive evolutionary feature (Dive & Eisenmann, 1991).

6.6 - POSTERIOR FIRST PHALANGES (TAB. 10)

There is no material from OIS 11 or OIS 8. The data for V5 and 10 on the OIS 6 material are not normally distributed (V5: n = 14, Shapiro-Wilk test statistic = 0.684, df = 14, p = 0.000; V10: n = 14, Shapiro-Wilk test statistic = 0.817, df = 14, p = 0.008). The Kruskal-Wallis test produces a significant result for both measurements (V5: n = 39, chi-square = 13.478, df = 2, p = 0.001; V10: n = 41, chi-square = 10.632, df = 2, p = 0.005). The ANOVA indicates that there is a significant difference in all measurements between phalanges from different oxygen isotope stages (tab. 11). The post-hoc tests show a significant difference between OIS 7 and OIS 6 for all measurements, between OIS 9 and OIS 6 in V1, 6 and 7, and between OIS 9 and OIS 7 in V6.

	Measurement	n	F	p
Anterior phalanges	V7	38	2.092	0.120
	V1	43	4.443	0.009
	V3	48	1.319	0.280
	V4	36	3.048	0.043
	V5	43	3.608	0.022
	V14	39	2.039	0.126
	V10	40	1.724	0.179
	V12	40	5.816	0.002
Posterior phalanges	V7	40	11.264	0.000
	V1	44	21.864	0.000
	V3	44	14.747	0.000
	V4	36	14.669	0.000
	V6	42	30.869	0.000
	V14	40	21.980	0.000
	V12	41	7.197	0.002

Tab. 11: Results of ANOVA of measurements on the anterior and posterior first phalanges (data from table 10).
Tab. 11 : Résultats de l'ANOVA à partir des premières phalanges antérieures et postérieures (données du tableau 10).

The log ratio diagram (fig. 6) shows that shape is similar in all three samples. The OIS 6 material is clearly smaller and slightly more robust (V3) than the material from OIS 9 and 7, whereas the OIS 9 material is relatively slender (V3, 4, 5, 6 and 14).

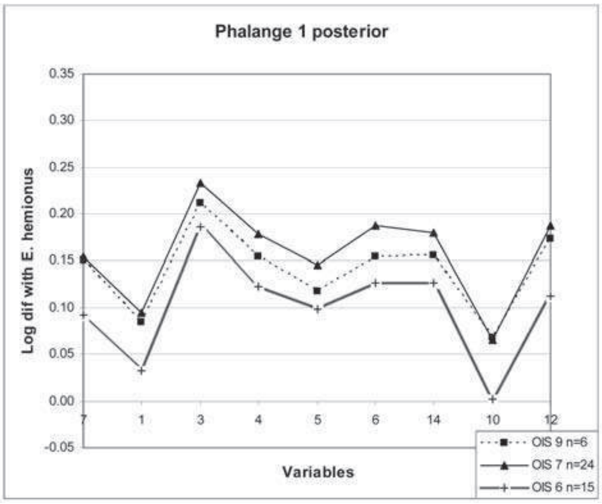

Fig. 6: Log ratio diagram of posterior first phalanges from the British Isles.
Reference line: *Equus hemionus* (data from table 10).
Fig. 6 : Diagramme des rapports des premières phalanges postérieures des îles britanniques. Ligne de référence : Equus hemionus *(données du tableau 10).*

7 - DISCUSSION

The changes in size and shape displayed by horses from the late Middle Pleistocene of the British Isles are complex. As the size and shape of the skeletal elements is influenced by a large number of factors, identifying the causes of a particular change in size or shape is not straightforward.

The relative sizes of the material from the different oxygen isotope stages show a similar pattern in the metapodials and the first phalanges. The material of OIS 11, 8 and 7 is large, whereas that of OIS 9 and 6 is small. The metatarsals of OIS 9 are relatively larger than the metacarpals, and to a lesser extent, this also holds for the metapodials of OIS 6. The size differences in the first phalanges are much less pronounced, although the limited amount of material precludes any definitive conclusions. In the dental elements, size differences are small between the OIS 11, 9 and 7 material, whereas the OIS 6 material is clearly smaller.

The large size of the OIS 11 horses can be attributed to their age, as the caballoid horses were large when they first evolved. In the metacarpals, the morphological characteristics that are influenced by long-term evolutionary trends are relatively advanced in the earliest horses studied here (OIS 11). The horses of OIS 9 are characterised by a return to a more primitive morphology. This could signify the migration of a population characterised by retention of or return to more plesiomorphic traits into the British Isles after the intervening glacial period of OIS 10. From OIS 8 onwards, a gradual development of the derived condition can be observed, culminating in the evolutionarily advanced OIS 6 horses. In the metatarsals, horses from all periods are of fairly advanced morphology, with the oldest horses (OIS 11) being the most primitive. The horses of OIS 6 show a flattening of the metapodials, which is an advanced evolutionary feature.

In the anterior first phalanges, the material of OIS 11 and 9 has relatively long infra-tuberosital segments, which is a primitive evolutionary feature (Dive & Eisenmann, 1991). In the more advanced material from OIS 7 and OIS 6, the infra-tuberosital segments are smaller relative to the supra-tuberosital segments.

It is unknown if and to what extent changes in locomotion result in detailed changes in morphology in the metapodials (Bignon *et al*., 2005). As the foreleg carries most of the weight and the hindleg mainly provides propulsion, the adaptations of the metacarpals and metatarsals are expected to differ. The distal keel of the metacarpals of OIS 11 and 9 is well-developed, whereas in the OIS 8, 7 and 6 horses, the distal keel is weakly developed. It is known that broad-legged animals live in humid environments, which would correspond well with the oceanic climate of OIS 11 and 9 (Shackleton & Opdyke, 1973; Foronova, 2006). However, on the metacarpals of the OIS 11 and 9 horses only the distal epiphysis is strongly developed. On the metatarsals, both epiphyses are well-developed in the OIS 11 horses, but in the OIS 9 horses, the distal epiphysis is only weakly developed. The diaphysis is slender in both the OIS 11 and the OIS 9 horses, and the posterior first phalanges are slender in the OIS 9 horses. The Type III protoconal index of the OIS 11 dental remains, thought to be indicative of a cool to cold climate, adds to the ambiguity.

The small size of the OIS 9 horses may be related to a combination of high temperatures and a high humidity (James, 1970). Alternatively, the scarcity of large carnivores in OIS 9 deposits (Schreve, 1997) may indicate lower levels of predation, resulting in a larger population competing for the same resources and a reduced selection pressure for larger body size. However, it should be kept in mind that there are only a few sites known that date from OIS 9 and therefore our knowledge of the fauna of this period is limited. The dental elements of these horses are relatively large when compared to the relative size of the limb elements due to the large genotypic influence on their size (Hillson, 2005). Instances of disproportion between dental elements and metapodials, with the teeth being either larger or smaller than expected from the size of the metapodials, have been observed in various Pleistocene assemblages (Eisenmann, 1988). The Type I protoconal index of the OIS 9 material is indicative of temperate conditions, which is in agreement with other environmental data for this period.

The weakly-developed sagittal keel and the relatively large breadths of the metapodials of the OIS 8, 7 and 6 horses may relate to the dry continental climate of all three phases (Ruddiman & McIntyre, 1982; Shackleton, 1987). The large body size of the horses of OIS 8 could be a corollary of the low temperatures, as an example of Bergmann's rule, whereas the large body size of horses in OIS 7 could have been induced by the continental and thus seasonal climate that characterised this interglacial (Blackburn *et al*., 1999). Temperate conditions are also implied by the Type I protoconal index of the OIS 7 material.

The OIS 6 horses have short, robust metapodials and first phalanges as an adaptation to the severe climatic conditions of this period. The protoconal index, which points to a Type II horse adapted to cold climatic conditions, is in agreement with this. The small size of the horses might have been induced by the severe conditions in which they lived, and this may imply a certain degree of isolation from populations in continental Europe.

8 - CONCLUSIONS

The study of horse remains from late Middle Pleistocene sites in the British Isles shows that horses displayed differences in size and shape throughout this period. The changes in size and shape do not appear to follow a unidirectional trend, but instead fluctuations can be observed, which can be interpreted as ecomorphological responses to the fluctuating climate of the late Middle Pleistocene. However, our knowledge of how climatic factors, coupled with characteristics of the horse population, horse behaviour and the composition of the fauna as a whole, influenced the size and shape of the horses is limited. Direct correlations of specific changes in size and shape with specific environmental factors or aspects of the animal community are therefore preliminary.

Long-term evolutionary processes produced gradual changes in the morphology of the metapodials and first phalanges. Changes in the dental elements, however, follow a different pattern from the changes in the leg bones. Because dental elements are influenced less by environmental factors and are more strongly controlled by genetic mechanisms (Hillson, 2005), they are less phenotypically plastic. The size of the dental elements thus remains relatively stable over the course of the late

Middle Pleistocene, with the exception being the OIS 6 horses, which can be characterised as a population under severe stress in a marginal environment. Changes in the protoconal index can be regarded as reflecting adaptation to differences in diet between cold and temperate conditions, although results for the analysis of this characteristic can be equivocal.

The horse populations of the various interglacial and glacial periods of the late Middle Pleistocene can be differentiated according to their size and shape. However, the horses of OIS 11, 8 and 7 are relatively similar in size and shape, although the limited amount of material does not allow for a definitive characterisation of the material of OIS 11 and OIS 8. When horse remains are analysed for biostratigraphic purposes, results from various skeletal elements need to be considered in conjunction, and of course all available information from other sources (e.g. geology, pollen analysis, absolute dating) should be taken into account.

It is to be expected that horse remains from mainland Europe, where climatic conditions were different from those in the British Isles for the greater part of the Middle Pleistocene, will not follow exactly the same pattern. Analysis of horse remains from the continent might shed light on migratory patterns and the processes that led to differences between the faunas of the British Isles and continental Europe. The research on the British material shows that horse remains can aid in establishing a biostratigraphic scheme. Study of horse remains from mainland Europe can potentially help solving the dating controversies surrounding some of the most important sites dating from the late Middle Pleistocene.

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REFERENCES

BIGNON O., 2003 - *Diversité et exploitation des équidés au Tardiglaciaire en Europe occidentale. Implications pour les stratégies de subsistance et les modes de vie au Magdalénien et à l'Azilien ancien du Bassin parisien*. Thèse de Doctorat, Université de Paris X, 856 p.

BIGNON, O., 2008 - *Chasser les chevaux à la fin du Paléolithique dans le basin parisien: stratégie cynégétique et mode de vie au Magdalénien et à l'Azilien ancien*. British Archaeological Reports International Series, **1747**, Oxford, 170 p.

BIGNON O., BAYLAC M., VIGNE J.-D., & EISENMANN V., 2005 - Geometric morphometrics and the population diversity of Late Glacial horses in Western Europe (*Equus caballus arcelini*): phylogeographic and anthropological implications. *Journal of archaeological science*, **32**, 375-391.

BLACKBURN T.M., GASTON K.J., & LODER N., 1999 - Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and distributions*, **5**, 165-174.

BOWEN D.Q., 1999 - *A revised correlation of Quaternary deposits in the British Isles*. Geological society special report, **23**, Bath, 174 p.

BRIDGLAND D.R., 1994 - *Quaternary of the Thames*. London, 441 p.

BRIDGLAND D.R., & SCHREVE D.C., 2001 - River terrace formation in synchrony with long-term climatic fluctuation: supporting mammalian evidence from southern Britain. *In* D. Maddy, M.G. Macklin & J.C. Woodward (eds.), *River basin sediment systems: archives of environmental change*. Lisse, 229-248.

CURRANT A., 1989 - The Quaternary origins of the modern British mammal fauna. *Biological journal of the Linnean society*, **38**, 23-30.

DIVE J., & EISENMANN V., 1991 - Identification and discrimination of first phalanges from Pleistocene and modern *Equus*, wild and domestic. *In* R.H. Meadow, & H.-P. Uerpmann (eds.), *Equids in the ancient world, Volume II*. Wiesbaden, 278-315.

EISENMANN V., 1979 - Les métapodes d'*Equus* sensu lato (Mammalia, Perissodactyla). *Géobios*, **12**, 863-886.

EISENMANN V., 1988 - Tentative typology and biostratigraphy of some Middle and Late Pleistocene western European horses. *Il Quaternario*, **1**, 103-109.

EISENMANN V., 1991a - Proportions squelettiques de chevaux quaternaires et actuels. *Géobios*, **13**, 25-32.

EISENMANN V., 1991b - Les chevaux quaternaires européens (Mammalia, Perissodactyla). Taille, typologie, biostratigraphie et taxonomie. *Géobios*, **24**, 747-759.

EMILIANI C., 1955 - Pleistocene temperatures. *Journal of Geology*, **63**, 538-578.

FORONOVA I., 2006 - Late quaternary equids (genus *Equus*) of South-western and South-central Siberia. *In* M. Mashkour (ed.), *Equids in time and space. Papers in honour of Véra Eisenmann.* Proceedings of the 9th conference of the International Council of Archaeozoology, Durham, August 2002, Oxford, 20-30.

FORSTÉN A., 1988 - Middle Pleistocene replacement of stenonid horses by caballoid horses - ecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **65**, 23-33.

FORSTÉN A., 1993 - Size decrease in Late Pleistocene-Holocene caballoid horses (genus *Equus*), intra- or interspecific evolution? A discussion of alternatives. *Quaternary international*, **19**, 71-75.

GASCOYNE M., CURRANT A.P., & LORD T.C., 1981 - Ipswichian fauna of Victoria Cave and the marine palaeoclimatic record. *Nature*, **294**, 652-654.

GEYH M.A., & MÜLLER H., 2005 - Numerical ^{230}Th/U dating and a palynological review of the Holsteinian/Hoxnian Interglacial. *Quaternary science reviews*, **24**, 1861-1872.

GIBBARD P., & VAN KOLFSCHOTEN T., 2004 - The Pleistocene and Holocene epochs. *In* F.M. Gradstein, J. Ogg & A. Smith (eds.), *A geologic time scale 2004*. Cambridge, 441-452.

GIBBARD P.L, BOREHAM S., COHEN K.M., & MOSCARIELLO A., 2005 - Global chronostratigraphical correlation table for the last 2.7 million years. *Boreas,* **34** (1), non paginé.

HILLSON S., 2005 - *Teeth*. Second edition, Cambridge, 388 p.

JAMES F.C., 1970 - Geographic size variation in birds and its relationship to climate. *Ecology*, **51**, 365-390.

KEEN D.H., 1995 - Raised beaches and sea-level in the English Channel in the Middle and Late Pleistocene: problems of interpretation and implications for the isolation of the British Isles. *In* R.C. Preece (ed.), *Island Britain: a Quaternary perspective*. Geological Society Special Publication, **96**, London, 63-74.

LISTER A.M., 1992 - Mammalian fossils and Quaternary biostratigraphy. *Quaternary science reviews*, **11**, 329-344.

MACFADDEN B.J., 1992 - *Fossil horses, Systematics, paleobiology, and evolution of the Family Equidae*. Cambridge, 383 p.

MADDY D., &. BRIDGLAND D.R, 2000 - Accelerated uplift resulting from Anglian glacioisostatic rebound in the Middle Thames Valley, UK?: evidence from the river terrace record. *Quaternary science reviews*, **19**, 1581-1588.

MITCHELL G.F., PENNY L.F., SHOTTON F.W., & WEST R.G., 1973 - *A correlation of Quaternary deposits in the British Isles*. Geological Society of London Special Report, **4**, London, 100 p.

MUSIL R., 1969 - Die Equiden-Reste aus dem Pleistozän von Süßenborn bei Weimar. *In* H. Wehrli (ed.), *Das Pleistozän von Süssenborn*. Berlin, 617-666.

NOBIS G., 1971 - Vom Wildpferd zum Hauspferd, Studien zur Phylogenie pleistozäner Equiden Eurasiens und das Domestikationsproblem unserer Hauspferde. *Fundamenta,* Reihe B, Band **6**, Köln, 96 p.

PENKMAN K.E.H., 2005 - *Amino acid geochronology: a closed system approach to test and refine the UK model*, Thèse de Doctorat, Université de Newcastle-upon-Tyne, 278 p.

RUDDIMAN W.F., & MACINTYRE A., 1982 - Severity and speed of Northern Hemisphere glaciation pulses: The limiting case? *Geological Society of America Bulletin*, **93**, 1273-1279.

SÁNCHEZ GOÑI M.F., TURON J.-L., EYNAUD F., SHACKLETON N.J., & CAYRE O., 2000 - Direct land/sea correlation of the Eemian, and its comparison with the Holocene: a high-resolution palynological record off the Iberian margin. *Netherlands journal of geosciences*, **79**, 345-354.

SAVAGE D.E., 1977 - Aspects of vertebrate paleontological stratigraphy and geochronology. *In* E.G. Kauffman & J.E. Hazel (eds.), *Concepts and methods of biostratigraphy*. Stroudsburg, 427-442.

SCHREVE D.C., 1997 - *Mammalian biostratigraphy of the later Middle Pleistocene in Britain*. Thèse de Doctorat, Université de Londres, 776 p.

SCHREVE D.C., & BRIDGLAND D.R., 2002 - Correlation of English and German Middle Pleistocene fluvial sequences based on mammalian biostratigraphy. *Geologie en mijnbouw*, **81**, 357-373.

SHACKLETON N.J., 1969 - The last interglacial in the marine and terrestrial records. *Proceedings of the Royal Society of London B*, **174**, 135-154.

SHACKLETON N.J., 1987 - Oxygen isotopes, ice volume and sea level. *Quaternary Science Reviews*, **6**, 183-190.

SHACKLETON N.J., & OPDYKE N.D., 1973 - Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core V28-238: Oxygen isotope temperatures and ice volumes on a 10^5 year and 10^6 year scale. *Quaternary Research*, **3**, 39-55.

SIMPSON G.G., 1941 - Large Pleistocene felines of North America. *American Museum Novitates*, **1136**, 1-28.

SIMPSON G.G., ROE A., & LEWONTIN R.C., 1960 - *Quantitative zoology*, Revised edition, New York, 440 p.

SONDAAR P.Y., 1968 - The osteology of the manus of fossil and recent Equidae, with special reference to phylogeny and function. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, afd. Natuurkunde*, Eerste reeks, Deel 25, **1**, 76 p.

SUTCLIFFE A.J., 1995 - Insularity of the British Isles 250 000 - 30 000 years ago: the mammalian, including human, evidence. *In* R.C. Preece (ed.), *Island Britain: a Quaternary perspective*. Geological Society Special Publication **96**, London, 127-140.

TURNER C., 1996: A brief survey of the early Middle Pleistocene in Europe. *In* C. Turner (ed.), *The early Middle Pleistocene in Europe*. Proceedings of the SEQS Cromer symposium, Norwich / United Kingdom / 3-7 September 1990, Rotterdam, 295-317.

TURON J.-L., 1984 - Direct land/sea correlations in the last interglacial complex. *Nature*, **309**, 673-676.

WHITE M.J., & SCHREVE D.C., 2000 - Island Britain - Peninsula Britain: palaeogeography, colonisation, and the Lower Palaeolithic settlement of the British Isles. *Proceedings of the prehistoric society*, **66**, 1-28.